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Brophy, C.; Finn, J. A.; Luscher, A.; Suter, M.; Kirwan, L.; Sebastià, M. T.; Helgadóttir, Á.; Baadshaug, O. H.; Belanger, G.; Black, A.; Collins, R. P.; Jure, Cop; Dalmannsdóttir, S.; Delgado, I.; Elgersma, A.; Fothergill, M.; Frankow-Lindberg, B. E.; Ghesquiere, A.; Golinska, B.; Grieu, P.

Published in:
Proceedings of the 27th General Meeting of the European Grassland Federation

Publication date:
2018

Citation for published version (APA):
Brophy, C., Finn, J. A., Luscher, A., Suter, M., Kirwan, L., Sebastià, M. T., Helgadóttir, Á., Baadshaug, O. H., Belanger, G., Black, A., Collins, R. P., Jure, C., Dalmannsdóttir, S., Delgado, I., Elgersma, A., Fothergill, M., Frankow-Lindberg, B. E., Ghesquiere, A., Golinska, B., ... Connolly, J. (2018). Identifying drivers of changes in relative abundances in agroecosystems. In B. Horan, D. Hennessy, M. O'Donovan, E. Kennedy, B. McCarthy, J. A. Finn, & B. O'Brien (Eds.), *Proceedings of the 27th General Meeting of the European Grassland Federation: Sustainable meat and milk production from grasslands* (Vol. 23, pp. 586-588). Teagasc.

Identifying the drivers of changes in the relative abundances of species in agroecosystems

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Abstract

Increasing species diversity often promotes ecosystem functions in grasslands, but sward diversity may be reduced over time through competitive interactions among species. We investigated the development of species' relative abundances in intensively managed agricultural grassland mixtures over three years to identify the drivers of diversity change. A continental-scale field experiment was conducted at 31 sites using 11 different four-species mixtures each sown at two seed abundances. The four species consisted of two grasses and two legumes, of which one was fast establishing and the other temporally persistent. We modelled the dynamics of the four-species mixtures over the three-year period. The relative abundances shifted substantially over time; in particular, the relative abundance of legumes declined over time but stayed above 15% in year three at many sites. We found that species' dynamics were primarily driven by differences in the relative growth rates of competing species and secondarily by density dependence and climate. Alongside this, positive diversity effects in yield were found in all years at many sites.

Keywords: biodiversity, dynamics, grass, legume, multispecies mixtures, relative growth rate

Introduction

The common practice of managing highly fertilised grassland monocultures has often been critiqued and there is a need for productive grass-legume systems that require less fertiliser and lead to improved environmental outcomes (Lüscher *et al.,* 2014, Suter *et al.*, 2015). There is wide consensus that increasing species diversity promotes many ecosystem functions. Over time, however, some species in a mixture may become dominant at the expense of others and sward diversity may decline, thus reducing the benefits to ecosystem function (Carroll *et al*., 2011). Here, we examine the dynamics of the relative abundances of multiple species in agronomic grassland mixtures and identify reasons why changes occur at the species level across 31 coordinated multi-year experimental sites.

Materials and methods

A common experiment was carried out at 30 sites across Europe and one site in Canada. At each site 22 four-species mixture plots were established. The four species comprised two grasses and two legumes, of which one was fast establishing and the other temporally persistent. Thus, there were four functional groups: grass (G) / legume (L) by fast establishing (F) / temporally persistent (P) which were denoted G_F, G_P, L_F and L_P. The identity of the species within functional groups varied across the sites; yet, there was a total of 11 unique species used across the experiment. At each site, the relative abundances of the four species were varied systematically across 11 mixture plots ranging from each species equally present (25% of each) to one species dominant (70%, 10%, 10%, 10%) and each of the 11 mixtures was sown at two seed abundance levels. Monocultures of each species were also established at each seed abundance level, giving an additional eight plots at each site. N fertiliser was applied at most sites (maximum rate of 150 kg N ha^{-1} annum) and plots were harvested between two and seven times per annum depending on local practice. The annual plot-level biomass of each of the four species was recorded for three years following the year of establishment. Further experimental details are available in Kirwan *et al.* (2007, 2014).

We analysed relative growth rates (Connolly and Wayne, 2005) for each species in mixture to explain changes in relative abundances for sown-year 1, years 1 - 2 and years 2 - 3.

Results and discussion

Across all sites, we found significant changes in the relative abundances of our four-species mixtures over the three years. The main driver of those changes was differences in the relative growth rates of species. On average across all sites, the temporally persistent grass (G_P) become dominant by year 3 (Figure 1) but the relative abundance of G_P in year 3 varied substantially across sites, ranging from 5% at one site to 100% at another (Brophy *et al.*, 2017). The relative abundance of legumes (L_F + L_P) was generally high in year 1, and while it declined over time, there were 12 sites that still had average legume abundance above 15% in year three. Legume persistence was positively related to sites' annual minimum temperature (computed as the average of the lowest five annual values) in years 2 (P = 0.002) and 3 (P = 0.003). Overall, we found several intra- and inter-specific density-dependent dynamics in our multi-species communities, which gave evidence for stabilising processes acting on the system (Brophy *et al.*, 2017). Alongside the substantial shifts in dynamics, Brophy *et al.* (2017) and Finn *et al.* (2013) showed significant positive diversity effects at many sites in all three years, the strengths of which were positively related to legume abundance.

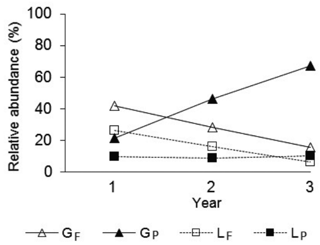

Figure 1. The average relative abundance of each functional group across all sites in each (post-seeding) year. The species are classified according to functional traits: fast establishing grass (G_F) and legume (L_F) and temporally persistent grass (G_P) and legume (L_P).

Conclusion

This continental-scale field experiment showed the importance of the relative growth rates of competing species for community dynamics and species shift over time. Alongside this, significant positive diversity effects were evident across the three experimental years at many sites. Diversity effects in multi-species mixtures can be further enhanced through the inclusion of legumes and strategic selection of the species and their cultivars, paying particular attention to their traits and competitive abilities relative to each other.

Acknowledgements

Support was received from Science Foundation Ireland, grant number 09/RFP/EOB2546, the European's Seventh Framework Programme (FP7/2007-2013; grant agreement no. 266018) and the EU Commission through COST Action 852.

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